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DEVELOPMENT OF *AMPHIOPLUS ABDITUS* (VERRILL) (ECHINODERMATA: OPHIUROIDEA): I. LARVAL BIOLOGY [1, 2]

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A novel pattern of ophiuroid development which involves the rapid direct development of an abbreviated pluteus-like embryo within a demersal fertilization membrane occurs in *Amphioplus abditus,* a burrowing shallow-water amphiurid of the east coast of the United States (Hendler, 1973). Development of *A. abditus* within a fertilization membrane, although resembling that found in certain sipunculids (Rice, 1967), polychaetes (Thorson, 1946; Davis, 1968), archiannelids (Ax, 1966), and holothuroids (Edwards, 1909; Ohshima, 1925), is previously unknown in ophiuroids and therefore warrents detailed description.

Materials and Methods

Specimens of *A. abditus* were collected from 1–3 m depths off Noank, Connecticut, at the northeastern end of Long Island Sound. Juveniles were reared during June and July, 1971 and 1972, from females which spawned naturally in the laboratory. Eggs were removed from fingerbowls with spawning females, transferred to small containers of millipore-filtered sea water, and immediately fertilized with freshly shed spermatozoa or sperm from stripped testes. Culture dishes routinely were held between 21° and 22° C in a running seawater bath. To test temperature tolerance, a culture initiated July 14, 1971, was held at 16° C. Culture water was replaced with fresh millipore-filtered sea water every other day.

Viable embryos identical to those reared in the laboratory were collected in the field from superficial sediment using SCUBA and the "Clarksucker", a small suction sampler (Clark, 1971). Observations were made on live specimens, using phase contrast; measurements were made with an ocular micrometer; and drawings prepared with the aid of a camera lucida.

Brine was prepared by freezing sea water, and dilutions of brine or sea water were used to test larval salinity tolerance. Seawater concentration required for successful hatching was gauged by subjecting mature ova, triangular embryos, circular ophiuroid disc, star-shaped ophiuroid disc stages, and newly hatched juveniles grown in 33‰ salinity sea water to 5, 10, 15, 20, 25, 30, 35, and 40‰ salinity. (The above developmental stages are described in Results). Three replicate tests were made of each of the combinations of eight salinities and four developmental stages and each replicate employed eggs from a single female. The

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subcultures were maintained in 50 ml beakers with 20 ml of test solution and 50–100 embryos (greater densities resulted in retarded growth). Every one to two days the solution in these cultures was changed. Numbers of embryos surviving or hatched were determined at 12- to 24-hour intervals by examination with a dissecting microscope, and these cultures were maintained up to ten days in order to test for survival.

Results

Development of Amphioplus abditus

Spawning. It usually is impossible to rear ophiuroid eggs stripped from ovaries. Forced spawning by exposing ripe individuals to artificial illumination after sunset (Grave, 1900; Mortensen, 1921, 1937; Olsen, 1942; Fenaux, 1963) or after dark-adaptation (Stancyk, 1973) is resorted to most frequently. On seven occasions female specimens of *A. abditus,* collected in the afternoon and held under constant illumination in unaerated sea water, spawned in the laboratory between 1800 and 0100 hours. This spawning after dark may have depended upon the time of collection, rather than an intrinsic nocturnal behavior pattern. Males held in a container with females generally shed spermatozoa after the females spawned. *Amphioplus abditus* was never observed while spawning during day or night dives, nor in laboratory tanks with sediment and running or standing sea water.

In fingerbowls with only seawater, their spawning posture is similar to that described for the burrowing species *Amphiura filiformis* (Mortensen, 1920; Woodley, 1975), *Amphiura chiajei* (Mortensen, 1920), and *Amphiodia barbarae* (MacGinitie and MacGinitie, 1949), an attitude described also in epibenthic species such as *Ophioderma brevispinum* (Grave, 1916), *Ophiopholis aculeata, Ophiura albida, Ophiura texturata, Ophiocomina nigra, Ophiothrix fragilis* (Olsen, 1942). The disc is raised several centimeters above the substrate by the proximal part of the arms, with the distal length of the arms radiating and flattened against the substrate to form a base. In their natural habitat this behavior would probably raise the disc above the sediment. The disc is never autotomized during spawning, ruling out the possibility that spawning results in natural loss of the disc and regeneration in amphiurid brittlestars (Clark, 1970).

During spawning, movement of the arms and oral skeleton produces waves of contraction superimposed on the rhythmical and strenuous contraction/relaxation of the muscles of the disc. These spawning labors are intermittent before, and continuous during shedding of gametes. Gametes are emitted simultaneously from all five bursae. The eggs are shed in loose streams and, although the proximal tube-feet move rapidly and might serve to carry gametes out of the ophiuroid's burrow, those shed in the laboratory fell directly to the substrate without contacting the tube-feet. Ova not immediately fertilized develop abnormally. Spermatozoa, also shed in strings, disperse rapidly and remain capable of movement for at least three hours.

Eggs are shed for about twenty minutes. Since all eggs are not shed in one spawning, and individuals are "spent" by August, there must be two or more spawnings during the two-month breeding period. Sperm is released spasmodically and the shedding time of males generally exceeds that of females, possibly an

adaptation to facilitate external fertilization, ensuring that sperm will be available throughout the period of egg release.

Egg maturation. Eggs which spawn naturally lack the germinal vesicles present in oocytes within the ovaries. One female (fixed during spawning, then embedded, and sectioned) had some oocytes with meiotic spindles within its ovaries. The oocytes were apparently shed during or shortly after the first meiotic division, as no polar bodies were seen until after fertilization. This may be a widespread phenomenon among ophiuroids, since polar bodies have been noted after fertilization for other species (Nachtrieb, 1885; Olsen, 1942; Fell, 1946), although observations in this regard for *Gorgonocephalus caryi* are equivocal (Patent, 1969).

The dark green-gray eggs are homolecithal. Newly-laid eggs are spherical or slightly ovoid and surrounded by extremely thin membrane(s). Within one minute after fertilization the outermost layer of the egg first becomes clear and then granular. Next, the fertilization membrane begins to expand away from the egg. As the perivitelline space enlarges, the surface of the egg wrinkles and its shape changes (Figure 1a). Simultaneously, the surface of the egg is covered with blebs which round off and then disassociate from the surface (Figure 1a). As they migrate and disappear, they seem to produce strands of material in the perivitelline space and leave stellar patterns on the fertilization membrane. These processes occur within 10 minutes, and within 30 minutes the egg again becomes spherical. It is usually eccentric within the expanding fertilization membrane and may be supported by cytoplastic elements from the cortical layer. Changes in the length of the egg (Figure 1a) indicate the extent of deformation during wrinkling. The length of major axis of the egg in microns (mean $\pm$ standard deviation, and number of measurements) changed from 132.12 ± 2.24 (10) for unfertilized ova; to 148.92 ± 1.41 (6) for wrinkled ova; and to 128.12 ± 2.00 (10) for ova after membrane elevation. The decrease in the diameter after fertilization was found to be significant using the Student-Newman-Keuls test.

Shortly after the ovum rounds off, the diameter of the fertilization membrane reaches a maximum of 417.88 ± 21.88 μ (s.d.). This leaves a perivitelline space in *A. abditus* of almost 150 μ, as compared with 10 μ in most other ophiuroids (Grave, 1898; Olsen, 1942; Patent, 1970) or 50 μ, at most (Narasimhamurti, 1933; Guille, 1964).

The expanded fertilization membrane of *A. abditus* is adhesive. Stickiness must be a property only of the expanded membrane since the newly shed eggs surrounded by a vitelline membrane are not adhesive. After the fertilization membrane is formed, and throughout development, the eggs adhere to the substrate. They stick to glass culture containers from which water has been decanted, and, if dislodged, they can settle and readhere.

The change in shape of the ovum of *A. abditus* following fertilization corresponds to the "angular phase" of *Ophiopholis aculeata* (Olsen, 1942) and may be part of a germinal localization process. However, the breakdown of the cortical layer, blebbing, wrinkling, and production of perivitelline structures are more exaggerated in *A. abditus* than in other echinoderms (Endo, 1961). The extremely expansive fertilization membrane may engage an unusual amount of material from the cortical layer since the mean egg diameter decreases 4 μ after wrinkling,

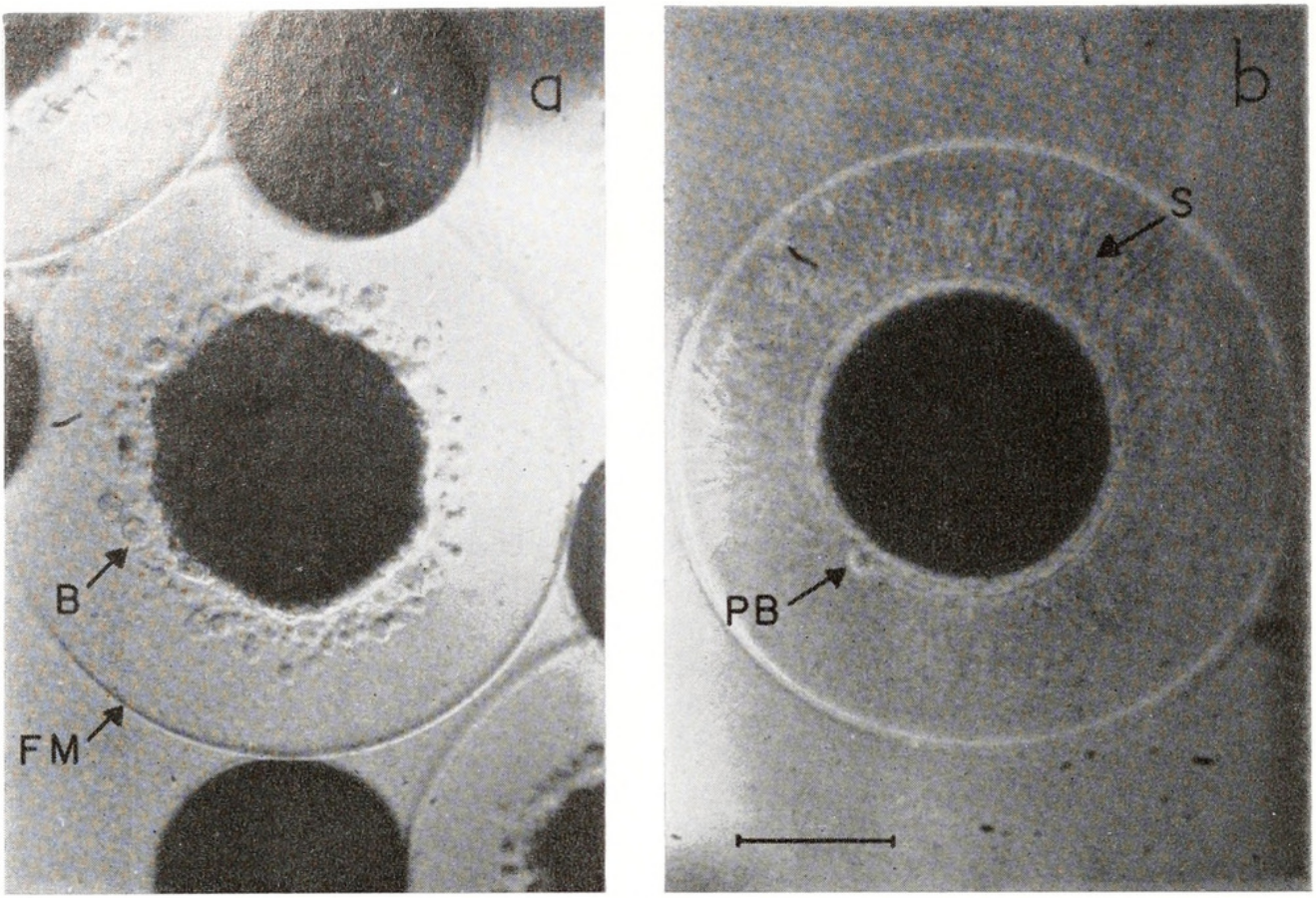

FIGURE 1. Ova of *Amphioplus* after fertilization: a shows an ovum at 16 minutes after fertilization, having irregular, nonspherical proportions, and blebs migrating toward the fertilization membrane; and b, an ovum at one hour, with nearly spherical shape and having strands of material in the perivitelline space and a newly extruded polar body. Scale line is 0.1 mm. Abbreviations are: B, blebs; FM, fertilization membrane; S, perivitelline strands; and PB, polar body.

suggesting loss of a 2 μ layer which might be converted to perivitelline material or the fertilization membrane.

Depending on temperature of the medium, the first polar body may be seen at 30 minutes and the remainder appear by one hour (Figure 1b). The polar bodies are extruded slowly, producing a bulge at the surface of the egg. They are found in a group on the surface of the egg and remain recognizable through the first 3 or 4 cleavages.

Cleavage, blastulation and gastrulation. The first segmentation occurs within 2 hours and the second follows in about 30 minutes, perpendicular to the first. Eight-cell and sixteen-cell stages are reached about 3 and 4 hours after fertilization, respectively. Successive divisions, equal and holoblastic, occur at approximately hourly intervals, producing a nonciliated blastula in 7–10 hours. A hyaline layer appears to invest each cell and does not seal the blastopore during gastrulation.

Gastrulation occurs within 9–12 hours, apparently by invagination, and the embryo afterward assumes a very blunt triangular shape with a small, rounded blastopore at the broad end. The blastopore broadens and widens as gastrulation continues and the embryo takes the shape of an arrowhead with the acute anterior end appreciably darker (denser) than the posterior.

Triangular embryo. By 16 hours after fertilization the embryo reaches a

length of 0.23 mm and is entirely ciliated. Embryos can move within the fertilization membrane at this time. In abnormal cases where the fertilization membrane is lacking, embryos are propelled across the bottom of the culture vessel by their cilia, but ordinarily, ciliary movement must serve only to circulate fluid within the fertilization membrane.

There are four important concurrent transformations between 18 and 24 hours. As the body reaches 0.28 mm, the posterior corners of the embryo protrude as rudimentary posterolateral arms (Figure 2a). The edges on either side of the blastopore, between the posterolateral protrusions, thicken and the blastopore is obliterated. Triradiate spicules, rudiments of the larval skeleton, appear near the posterolateral protrusions. Toward the apex of the embryo, the anterior end, the hydrocoel becomes visible as a curved, five-scalloped structure.

The embryo assumes a recognizably new and distinct form after 30 hours of development (Figure 2b). It has reached its maximum length, but the posterolateral arms extend almost perpendicular to the body so that the width exceeds

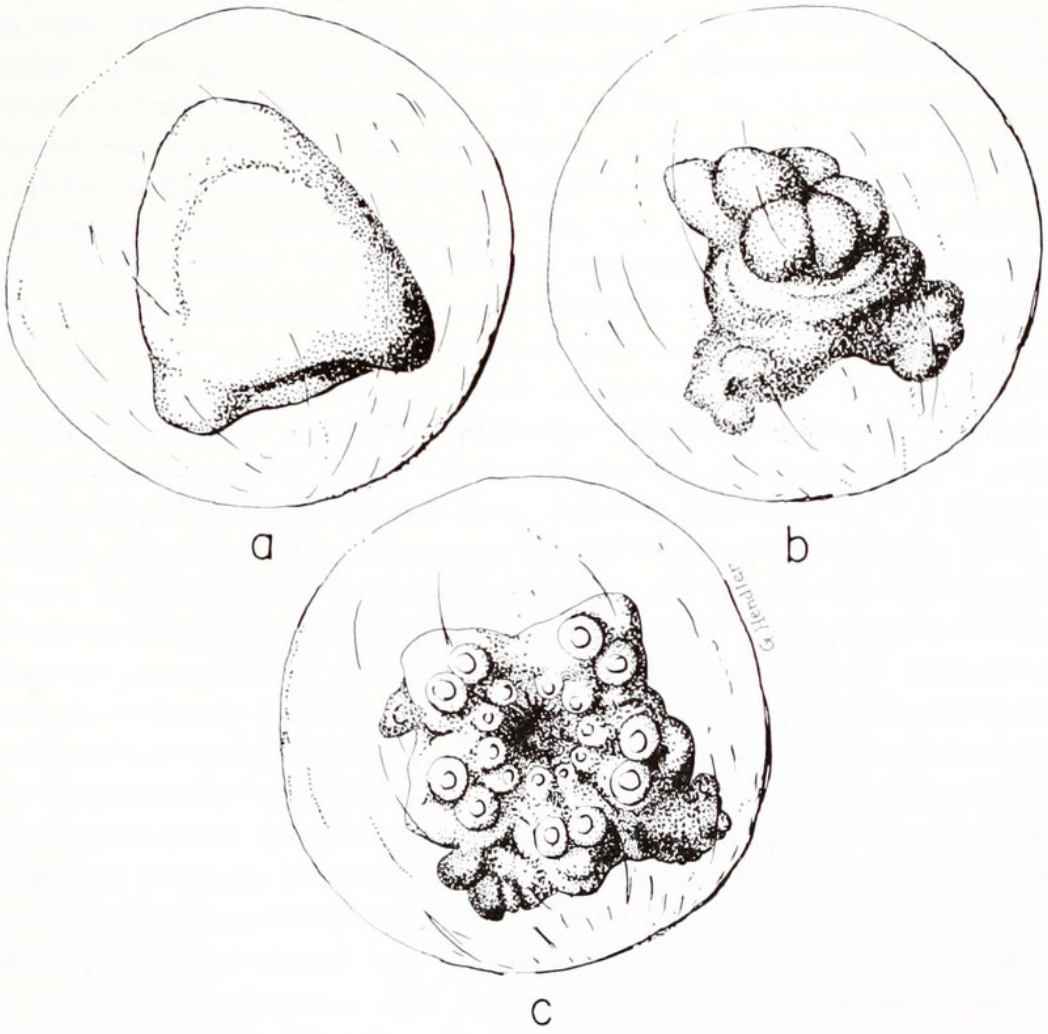

FIGURE 2. Major embryonic stages of *Amphioplus*. Neither perivitelline structures nor ciliation are shown, but fertilization membranes are illustrated. Embryos are each approximately 0.3 mm long, and fertilization membranes about 0.4 mm diameter. Drawing a shows an advanced triangular embryo with rudimentary posterolateral arms and an elevated area surrounding the hydrocoel, 24 hours; b, an early circular disc stage with emerging opiuroid rudiment and plamate embryonic arms, 34 hours; and c, star disc stage with reduced embryonic structures and a prominent ophiuroid rudiment having podia and mouth.

the length. The anterior ventral surface of the body bulges and beneath the protrusion there is a hydrocoel with five large lobes. The larval skeleton, extending to the base of the arms, has become tetraradiate, elongate, and bilaterally symmetrical. Cilia still cover the entire body but are most noticeable on the arms.

Circular ophiuroid disc. Between 34 and 38 hours the ophiuroid rudiment emerges as a circular disc on the embryo (Figure 2b). An indentation, the presumptive mouth, appears at the center of the disc and five lobes form along the edge of the disc. The tips of the embryonic arms become indented, giving them a palmate appearance, and the only prominent ciliation is on the distal edges of the arms.

The five radii of the disc clearly indicate the rudimentary ophiuroid arms by 40 hours. Shortly afterward, 20 tube-foot rudiments can be distinguished, two on each side of each presumptive arm. The distal pairs are larger, and appear to form earlier, than the proximal. This indicates that the ends of the hydrocoel have already fused below the enlarging ophiuroid mouth. At this stage the tips of the larval skeleton bifurcate and the ophiuroid skeleton consists of six triradiate primary plates, five tetraradiate terminal plates, and ten to twelve tiny rudiments of the oral skeletal elements. The shape of the ophiuroid body becomes even clearer by 45 hours as the arm tips sharpen and the tube-feet become erect papillae. The embryonic body becomes less prominent, with the embryonic arms scarcely wider than the ophiuroid body. At the same time, the larval skeleton continues to grow, becoming more clearly visible as yolk reserves are depleted, and the embryonic arms become transparent.

Star-shaped ophiuroid disc. As the ophiuroid disc rudiment takes a pentagonal shape, the mouth, tube-feet, and arms enlarge (Figure 2c). The anterior tip of the embryonic body and the embryonic arms, still paddle-shaped, become smaller and increasingly transparent, while the larval skeleton becomes more complex. Cilia, sparse but still active on the larval armtips by 50 hours, continue to disappear from the body. The tube-feet, the first part of the ophiuroid rudiment to move, begin to wave at about 55 hours. The more proximal tube-feet are shifted toward the enlarging oral cavity and increased transparency in the buccal area indicates the stomach is enlarging. By this time ophiuroid skeletal elements have advanced in size by branching, but the larval skeleton is noticeably simpler by 60 hours and the anterior tip of the larval body takes on a pinched papillate shape owing to resorption. Within another few hours the ophiuroid body begins to move and the increased coordination of the musculature of the body matches a concomitant increase in the complexity of the ophiuroid skeleton.

By 70 hours of development the triangular gastrula shape is obscured by the pentagonal ophiuroid form. The apex of the embryo is insignificant; embryonic arms are small, clear, and devoid of ciliation; and the larval skeleton diminishes. The ophiuroid skeleton continues to branch and anastomose, forming plates of solid outline, and the tube-feet lengthen. Between 75 and 85 hours, the total resorption of embryonic structures and the development of the juvenile ophiuroid occur *pari passu*. During this period the ophiuroid is increasingly active. It moves about within the fertilization membrane, often buckling the membrane as it retracts its tube-feet. The terminal plates of the arm also distort the shape of the membrane and sometimes scratch it.

Hatching and juveniles. Hatching, the escape from the fertilization membrane, may begin within 90–95 hours and in a single culture may continue for several days. Since the young are at the same stage of development, the prolonged period of hatching must be a function of the strength of the fertilization membrane or of the juvenile. Emergence is through a slit in the fertilization membrane, probably produced by the pressure of the terminal plates. During emergence the tube-feet are used to push against the membrane and pull on the substratum. The fertilization membrane is discarded and not used as food.

Newly hatched juveniles with disc diameters of 0.3 mm (radius from mouth to tip of arm = 0.21 mm) move about continually. They walk on the distal podia (second buccal tube-feet of the adult), often rearing up, raising the entire body on a pair of podia and sometimes using the adoral shield spines for leverage. In fingerbowls they usually concentrate on the bottom edge but sometimes climb or float upside-down under the surface film. Offered fine sediment, they alternately move across the surface and burrow.

The podia are adapted in shape and secretory ability for locomotion. Distinct patches on the column and the entire tip of the podia, as well as the epidermis bordering the edge of the disc, stain metachromatically with toluidine blue, indicating localized mucous production. In addition, the tips of these ambulatory podia (not the terminal or first buccal tube-feet) possess two plus three opposing papillae. These are lacking from podia of adult specimens and they may be a modification to increase surface area of the tips of the juvenile's tube-feet for increased traction. Detrital material adheres primarily to the tube-feet of juveniles, whereas in adults the spines are more important than tube-feet as mucous-secreting structures.

Juveniles lose the green coloration of the egg and embryo as the skeletal plates enlarge. Within two weeks, detrital material is ingested giving the stomach a deep-brown color and causing the disc to bulge upward.

Growth in the laboratory is very slow. Juveniles hatched in July, and maintained at 15° C from the end of August, produced one arm-segment in 2 months, three at about 3 months, and four by 8 months. Although conditions for growth were probably not optimal, the temperature was higher than that in the field over the winter so that accelerated growth might have been expected. The growth rate differs from Mortensen's (1920) observation that *Amphiura filiformis* reaches the 4 arm-segment stage in 4 months in both laboratory and field. Even the 4 to 8 arm-segment stages of *A. abditus* have tube-feet with papillate tips and move on the tube-feet rather than by movement of the arms. They progress with one arm leading and two trailing, moving alternately under or on top of the sediment. Evidently the adult habit of maintaining a burrow is not adopted until a larger size is attained.

Embryonic tolerance

Temperature. Development was faster in cultures raised at 21° C than at 16° C. Cultures at 16° C developed only to a point where the embryonic body was nearly resorbed; they reached this stage (normally found by 84 hours) at 156 hours, failed to hatch, and died at nine days after fertilization, probably due to exhaustion of food reserves. Q_{10} for rate of development calculated for different

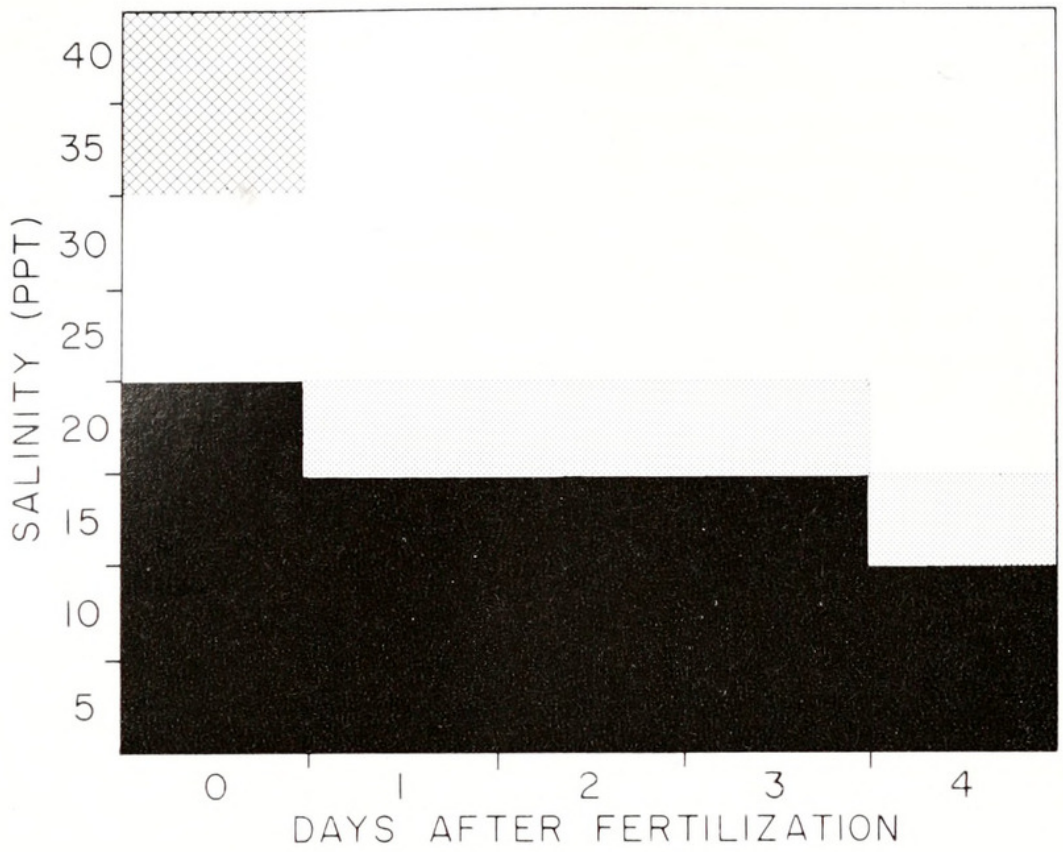

FIGURE 3. Success or failure of hatching for five developmental stages raised at eight salinities. The stages transferred to test salinities were: mature ova, 1.5 hours; triangular disc, 12 hours; circular ophiuroid disc, 12 hours; star-shaped ophiuroid disc, 36 hours; and newly hatched juveniles, 96 hours. Black represents 100% mortality; stippled, swelling of tissues but all replicates with some hatching success; white, all replicates with extensive hatching success; cross-hatched, two of three replicate cultures with 100% mortality.

stages from gastrulation to movement of podia decreased from 5.7 to 2.3. This indicates that development is temperature sensitive and especially so during early stages of morphogenesis. The failure of cultures to develop at 16° C while ambient field temperatures at the same time were 18° C indicates that small temperature changes may have a critical role in the survival of the species. The temperature-limited stage of the life history is in the embryo, since the adult, in the course of the year, survives 0–25° C and tolerates refrigeration in the laboratory during the summer.

Salinity. Tests of salinity tolerance of *Amphioplus* embryos revealed optimal survival at 25–30‰ salinity sea water. The mortality of embryos was elevated in solutions more concentrated or dilute, with the highest mortality in the most hypotonic solutions tested. The results of these tests are shown in Figure 3. For example, reading the axis for 1-day (12-hr) embryos: dilutions of 5–15‰ were lethal (black band); 20‰ resulted in swollen embryos as a result of osmotic stress, but these cultures hatched; and salinities of 25–40‰ gave normal development and hatching.

In general, salinities of at least 20 and preferably 25–40‰ are necessary for survival. In stages less than one day old, the tolerance range is restricted to 25–30‰ and two of three replicate cultures did not survive 35–40‰. On the other hand, after hatching, tolerance to osmotic stress expands to a range of

15–40‰. This pattern of broadening tolerance is found in other organisms (Kinne, 1964).

Marginally hypotonic sea water caused swelling of tissues within 12 hours. Mortality was greater in cultures at marginally low salinities than in isotonic cultures. In extremely hypotonic solutions cells blanched and disintegrated while fertilization membranes often expanded and sometimes ruptured. At 15‰ the cells of early stages sometimes expanded, but usually separated and then dissolved. At the same salinity, the development of advanced stages stopped and superficial structures sometimes swelled to fill the entire fertilization membrane before the embryo disintegrated.

Mature *A. abditus* transferred from the field to bowls with sea water in different concentrations showed a tolerance range similar to that shown by the juveniles raised in the laboratory, indicating that salinity is equally limiting to all but the earliest stages of development. For adults, salinities of 0–5‰ and 50–75‰ were immediately lethal. Those in 10–15‰ showed irritability for a day before dying but only salinities of 20–40‰ were tolerated for the 36-hour test period.

Discussion

Amphioplus abditus has a superficially orthodox morphogenesis and passes through a reduced pluteus-like stage with vestigial embryonic arms, ciliation, and skeleton. It resembles free-swimming ophioplutei both in the median, ventral origin of the stomodeum and closure of the blastopore, although it lacks a functional embryonic anus and the genesis of the coelom is not fully understood.

Modifications in morphogenesis and the elaboration of a formidable fertilization membrane are involved in the rapid, direct, and dermersal development of *A. abditus* within a fertilization membrane. The chronology of development in free-swimming ophiopluteus larvae suggests that completion of the larval body generally takes one to two weeks while complete metamorphosis takes about a month (Hendler, 1975). Thus, abbreviated development in *A. abditus* must result from accelerated morphogenesis of the ophiuroid rudiment *as well as* the virtual absence of a complex larval body. If only the latter were important, complete development would take two weeks rather than one. This dispatch depends on the economy of direct development with a supply of yolk that eliminates the necessity of feeding, nutrient transfer, and the maintenance metabolism of a complex, active larval body.

The important attributes of the fertilization membrane: its size, strength, and adhesiveness are initimately associated with the mode of direct development of *A. abditus*. The first two properties are prerequisites for direct development *per se*. Fertilization membranes of most ophiuroids enclose minimal perivitelline space and are presumably weakened or dissolved by a hatching enzyme as in echinoids (Kumé and Dan, 1968) and discarded by the ciliated, motile larva. There are several possible mechanisms that restrict *A. abditus* to the fertilization membrane: first, the size of the envelope relative to the embryo and the perivitelline material produced by the cortical bodies prevent mechanical breakage; and secondly, the embryo may lack a hatching enzyme or the membrane may be resistant to such an enzyme. The membrane is resilient, not easily ruptured without injuring

the embryo. Naturally, size and strength of the membrane and direct development protect the embryo from physical factors and injury by microorganisms. The fact that the fertilization membrane expands to 0.4 mm must discourage predation by meiobenthic fauna that could destroy an unprotected 0.15 mm zygote. Density of the egg and adhesiveness of the fertilization membrane are responsible for demersal development, because they result in sinking of the egg and restrain its movement along the bottom.

In the field, developing embryos were occasionally recovered from containers set about 0.5 m off the bottom to collect settling plankters. Embryos in various stages of development were recovered from the surface of the sediment, but were never taken in the plankton sampled by pump or townet. This indicates that the eggs, embryos, and possibly juveniles, though not planktonic, may be dispersed for short distances by bottom disturbances or currents.

The salinity tolerance of larval and adult specimens of *A. abditus* (roughly 20–40‰) is as broad as many estuarine organisms and approaches the lower limit for echinoderms (Kinne, 1964; Binyon, 1966). Though echinoderm larvae are notoriously less tolerant to low salinity than larvae of lamellibranchs, gastropods, and polychaetes, the rapid demersal development of *A. abditus* suits it for estuarine conditions (Thorson, 1946). For the Mystic River estuary where *A. abditus* was collected, the salinity in vertical transect ranges from 3–30‰ (Pearcy and Richards, 1962). *Amphioplus abditus* cannot tolerate this range and survives where it can avoid salinity stress. The eggs adhere to the bottom where the estuarine salinity is highest and temperature and salinity are least variable; restricted dispersal keeps embryos in a suitable milieu, and rapid development reduces exposure to temperature and salinity fluctuations. Accurate temperature and salinity tolerances have been measured for the larvae of only one other echinoderm, the asteroid *Acanthaster planci*. Lucas (1973) found that *A. planci* had a narrow thermal tolerance but a higher optimum temperature than *A. abditus*. Interestingly, *A. abditus* develops at salinities 20‰ or greater, while *A. planci* required at least 26‰. These differences are not unexpected considering the contrasting environments of the two species: temperate lower estuary and tropical coral reef.

Larvae of estuarine organisms are commonly found to have adaptations to limit their dispersal and evidence is accumulating that demersal development is sometimes adopted (Carriker, 1967; Mileikovsky, 1971; Stancyk, 1973). *Thyone briareus*, a holothuroid commonly sympatric with *A. abditus*, has an abbreviated development within the fertilization membrane (Ohshima, 1925), and it is expected that rapid demersal development within the fertilization membrane will be found for other echinoderms in waters of low salinity.

Direct development in the fertilization membrane may have been found, but not recognized as such, in other ophiuroid species. Nachtrieb (1885) described but did not figure the development of *Ophiophragmus wurdemani*, a shallow-water species from North Carolina and Florida, whose development seems strikingly similar to *A. abditus*. Nachtrieb indicates that the larvae hatch within several days but does not mention a fertilization membrane. Kirk (1916) and Fell (1941) describe an embryo for an unknown ophiuroid species from New Zealand which develops within a "perfectly transparent, thin but extremely tough

chitinous envelope . . . deposited in irregular clusters of from 10 to 100 or more" (Kirk, 1916, p. 383). Whether this envelope is a fertilization membrane is yet unknown.

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Summary

1. *Amphioplus abditus,* a burrowing, shallow-water amphiurid brittlestar of the eastern coast of the United States, has a nonplanktonic development within an adhesive, demersal fertilization membrane.

2. The embryo is a ciliated pluteus-like form with a transient blastopore, and vestigial larval arms and skeleton.

3. Development, which takes place on the surface of the sediment, is completed within four days at usual spawning temperature and the slow-growing post-larva, about 0.3 mm disc diameter, is active and capable of burrowing and feeding.

4. Salinity of at least 20–25‰ is necessary for embryonic development and adult survival, but temperature appears to be more critical for embryos than adults and may be an important limiting factor for the geographical range of the species.

5. Rapid, demersal, abbreviated development is an adaptation to a fluctuating, low-salinity environment as it restricts the embryo to the sediment-water interface where salinity is maximal and temperature and salinity are relatively constant. This mode of development has the advantages of direct development but permits limited dispersal capability.

6. The rapid rate of development is attributed to *both* accelerated morphogenesis and the virtual absence of a complex larval body.

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